AN EXAMINATION OF THE CLASSIFICATION OF SOME AUSTRALIAN MEGASCOLECID EARTHWORMS (ANNELIDA: OLIGOCHAETA) BY NUMERICAL METHODS

CARDEN C. WALLACE

Queensland Museum

ABSTRACT

Forty-nine species of Megascolecid earthworms (Annelida: Oligochaeta: Megascolecidae), at some stage included in the genera *Plutellus* Perrier and *Woodwardiella* Stephenson, were examined by numerical methods using information statistic and Euclidean strategies. Both dendrograms and ordinations were obtained, and the groupings seen in these agreed to a large extent with groupings recently proposed by Jamieson. In an attempt to assess the contribution made to the classification by four quantitative attributes (ratios of intersetal distances to body circumference), the programmes were repeated without these attributes; their removal had little effect on the results at the 'probably generic' level, and a slight effect on the intensity of clustering above this level.

The Australian Megascolecidae (Oligochaeta) are at present under review by Jamieson. Part of this work (1970, 1971a, c, 1972a, b, c) examines the relationships among species previously placed in (or ascribable to in the case of new species) the genera *Plutellus* Perrier and *Woodwardiella* Stephenson. Comparisons between members of the two genera have not previously been made, despite obvious similarities among some of the members, because of the importance attached to the 'key' character of prostate morphology. (In a similar way comparisons between groups with conflicting setal arrangement is rarely attempted.) The present study takes advantage of Jamieson's groupings to test the usefulness of numerical methods of taxonomic analysis in a review of this nature. Computer programmes for mixed-data taxonomic analysis are available in Australia, and as the number of Australian Megascolecid species is large (Jamieson, 1971c lists 247, and most collecting in uncollected areas yields undescribed material), a numerical method of analysis would be an advantage.

THE GROUP UNDER STUDY

The type-species of the genus *Plutellus*, *P. heteroporus* Perrier, is enigmatic, and almost a typological classic. It was described in 1873 from two specimens in the Paris Museum, collected over fifty years before (Macnab and McKey-Fender, 1948). Its locality was given as Pennsylvania, but no similar material has since been collected from that region. The validity of the type-locality has been questioned by Gates (1961, 1962) on zoogeographical

grounds, and by Jamieson (1970), who shows a close morphological similarity between *Plutellus heteroporus* and the New South Wales *P. manifestus* (Fletcher); Paris Museum collections included Australian material at the time Perrier was working.

The more obvious morphological features of *P. heteroporus*—the 'lumbricin' setal arrangement (eight setae per segment), tubular prostates emptying as a single pair of male pores with the male ducts on segment XVIII, and the holonephric nephridial system—were regarded as distinctive, and became the necessary characters for admission into the genus. Michaelsen (1900) gathered into the genus all material satisfying these requirements. This included North American material formerly of the genus *Argilophilus* Eisen, Australian material formerly *Cryptodrilus* Fletcher, *Megascolides* McCoy, and *Notoscolex* Fletcher, and two Ceylon species of *Megascolides*. The Australian genus *Fletcherodrilus* Michaelsen was added to the group by Michaelsen (1910) despite the fact that its male pores were unpaired.

Since then, other authors, in particular Gates and Macnab and McKey-Fender, continued ascribing new material to the genus, though always noting the need for revision, until the number of species reached approximately 105, with a distribution including Australia, Tasmania, New Caledonia, New Zealand, Auckland Islands, Queen Charlotte Island, the Pacific Coastal strip of North America, Guatemala, northern South America, India, Ceylon and Burma (Jamieson, 1971c).

Gates (1961) considers oriental species to be distinguished by a lack of calciferous glands, and Burmese species to be possibly congeneric with these; in 1962 (p. 187) he regards the genus as 'a congeries which has in common only the two characters of its family (Acanthodrilidae, *sensu* Gates) and in addition the lumbricin arrangement of the setae', and its distribution 'as incongruous as the morphology'. McKey-Fender (1957, p. 58) notes that 'so much remains to be done, of even a very elementary nature in the study of this genus'. The fact that the problem was not immediately seized upon is probably indicative of the very small number of taxonomists interested in oligochaete classification.

The first contribution to a revision of the genus was made by Jamieson (1970), who found clear indications of morphological affinities between *Plutellus manifestus* and certain members of the genus *Woodwardiella*, to which he gave generic status as *Heteroporodrilus*. The two genera, because of their possession of different types of prostate gland structure, had previously been placed in different families (the Acanthodrilidae and Megascolidae, *sensu* Gates, respectively). Jamieson proposed that *Plutellus* be restricted, possibly to contain only *P. manifestus* and *P. heteroporus*, that *Argilophilus* be reinstated for the North American species, and that the rest of the genus be examined for further groupings. *Fletcherodrilus* was later reinstated (Jamieson, 1971c), and a new species described from Lord Howe Island, previously ascribable to *Plutellus*, was given the new name of *Paraplutellus* Jamieson, 1972a.

The next stage in the breaking-down of the Australian *Plutellus* was the grouping of a number of species with Victorian distribution under a new generic heading, *Simsia* Jamieson, 1972a, b. Within this grouping he showed some species to be synonymous—*Megascolides steeli* Spencer with *Simsia manni*, *M. attenuatus* Spencer and *M. incertus* Spencer with *S. minor*, and *M. roseus* Spencer with *S. tuberculata*. The Western Australian species were separated off as a genus, *Graliophilus*, within which five species-groups are defined (Jamieson, 1972c). The most distinctive of these groups, the '*georgei*' and '*strelitzi*' groups, are suggested to be of possibly generic status.

Of the Australian *Plutellus*, this leaves some seventeen species unplaced, although the number for which material is available is now considerably less than this. In order to examine the affinities of Australian *Plutellus* species, this study included as many as possible of the following: *Heteroporodrilus* and *Woodwardiella* sens. strict. members; Australian, North American and oriental *Plutellus* (*sensu* Michaelsen) members; *Fletcherodrilus* and *Paraplutellus*. This group was entitled for the convenience of the study, the 'plutelloids'.

Previous Applications of Numerical Taxonomy to Oligochaetes

Three authors have applied numerical methods in revising Oligochaete classifications. Sims (1966, 1969) used the methods of Sheals (1964) to study relationships agmonst 29 Megascolecid genera, and achieved a classification similar to that proposed earlier by Gates (1959). Sims's work is interesting as a tentative application of numerical methods to an Oligochaete classification and it is cited by Mayr (1969, p. 211) as a demonstration of 'the utility of the phenetic approach'. However it has been criticized by Lee (1970) for its use of inappropriate taxa, and Sims's interpretation of results have been shown to be susceptible to a different interpretation by Jamieson (1971b). In a later paper (1971) Sims applied similar techniques to a classificatory problem in the family Eudrilidae. He effectively demonstrates the futility of classificatory schemes based on intuitive emphasis on a particular characteristic, at least in this family, where affinities based on any one structure have no correlation with affinities based on other structures.

Lee (1970) in an analysis of New Zealand Megascolecidae, avoided the faults he saw in Sims's treatment of the family by employing a more comprehensive taxa list. He used the information statistic of Lance and Williams (1967), and obtained groupings which substantially endorsed his own earlier (1959) classification.

Jamieson (1968) examined members of the family Alluroididae. A single similarity matrix was subjected to three clustering strategies. Computations were done by desk computer, necessitating binary coding of data. For example, in order to code numbers and positioning of spermathecae, five questions requiring yes/no answers were required. More recent taxonometric programmes allow coding of non-metrical characters with much less distortion to 'fit' a coding format (for example Burr, 1968, 1970; Watson, Williams and Lance, 1967; Lance and Williams, 1967). Jamieson has also used methods similar to those described in the present paper to examine the usefulness of setal ratios as indicators of overall phenetic similarity at various taxonomic levels (Jamieson, 1972b, 1972d; Jamieson and Bradbury, 1972). In the groups he has studied, Jamieson has been able to show setal ratios to have the following qualities: (a) little intraspecific variation, any variation being mainly of an inter-populational nature; (b) reasonable homogeneity within genera, although not always good differentiation between genera of the same suprageneric group; and (c) strong similarities within and distinctness between suprageneric groups.

METHOD

Two tasks were planned: firstly, to examine groupings within an available plutelloid set, using as complete an attribute list as possible, and secondly to observe the effect of removing a small number (four) of 'highly rated' attributes from the study.

TABLE 1

O.T.U.'s Studied from the 'Plutelloid' Group

O.T.U. No.	Original name	Genus * (pre-revisional)	Grouping * (after Jamieson)
1	*Megascolides attenuatus* Spencer, 1892	Pu	S (<15)
2	*Plutellus candidus* Jackson, 1931	Pu	G (s)
3	*Megascolides eucalypti* Spencer, 1900	Pu	S
4	*Cryptodrilus fasciatus* Fletcher, 1889	Pu	F
5	*Cryptodrilus frenchi* Spencer, 1892	Pu	U
6	*Graliophilus georgei* Jamieson, 1971	—	G (g)
7	*Cryptodrilus hobartensis* Spencer, 1895	Pu	U
8	'*Megascolides incertus*' Spencer, 1892	Pu	S†
9	*Cryptodrilus insularis* Spencer, 1895	Pu	U
10	*Cryptodrilus intermedius* Spencer, 1892	Pu	S
11	*Cryptodrilus lucasi* Spencer, 1892	Pu	S
12	*Cryptodrilus macedonensis* Spencer, 1892	Pu	U
13	*Cryptodrilus manifestus* Fletcher, 1889	Pu	P
14	*Megascolides manni* Spencer, 1892	Pu	S
15	*Cryptodrilus minor* Spencer, 1892	Pu	S
16	*Cryptodrilus oxleyensis* Fletcher, 1889	Wa	H
17	*Megascolides roseus* Spencer, 1892	Pu	S (<24)
18	*Cryptodrilus semicinctus* Fletcher, 1890	Pu	U
19	*Megascolides steeli* Spencer, 1900	Pu	S (<14)
20	*Plutellus strelitzi* Michaelsen, 1907	Pu	G (s)
21	*Cryptodrilus tanjilensis* Spencer, 1892	Pu	U
22	*Notoscolex tasmanianus* Fletcher, 1888	Pu	U
23	*Megascolides tisdalli* Spencer, 1900	Pu	S
24	*Notoscolex tuberculatus* Fletcher, 1888	Pu	S
25	*Cryptodrilus ? unicus* Fletcher, 1889	Pu	F
26	*Cryptodrilus victoriae* Spencer, 1892	Pu	U
27	'*Cryptodrilus willsiensis*' Spencer, 1892	Pu	S‡
28	Mt Macedon B	—	—
29	*Plutellus adecus* Macnab and McKey-Fender, 1959	Pu (t)	A
30	*Plutellus blacki* Macnab and McKey-Fender, 1952	Pu (d)	A
31	*Plutellus davisi* Macnab and McKey-Fender, 1952	Pu (d)	A
32	*Plutellus fenderi executus* Macnab and McKey-Fender, 1958	Pu	A
33	*Plutellus fenderi fenderi* Macnab and McKey-Fender, 1958	Pu	A
34	*Plutellus heteroporus* Perrier, 1873	Pu	P
35	*Plutellus hyoiedes* Macnab and McKey-Fender, 1959b	Pu (t)	A
36	*Plutellus macnabi* McKey-Fender, 1957	Pu (A)	A
37	*Plutellus panulirus* Macnab and McKey-Fender, 1959a	Pu (d)	A
38	*Paraplutellus insularis* Jamieson, 1972	—	PP
39	*Simsia longwarriensis* Jamieson, 1972	—	S
40	*Woodwardiella ashworthi* Stephenson, 1931	Wa	H
41	*Cryptodrilus canaliculatus* Fletcher, 1889a	Wa	H
42	*Cryptodrilus cooraniensis* Spencer, 1900	Wa	H
43	*Woodwardiella dioecia* Stephenson, 1933	Wa	H
44	*Heteroporodrilus lamingtonensis* Jamieson, 1970	Wa	H
45	*Cryptodrilus mediterreus* Fletcher, 1889	Wa	H
46	*Cryptodrilus shephardi* Spencer, 1900	Wa	H
47	*Cryptodrilus tryoni* Fletcher, 1889b	Wa	H
48	*Plutellus varicystis* Jackson, 1931	Gu	G (g)
49	*Woodwardiella molaeleonis* Michaelson, 1907	Wa	W

CHOICE OF MATERIAL

The material consisted mainly of the most recent literature descriptions of the species. In addition, for Australian material and *Plutellus heteroporus*, the author's nephridial descriptions were used, and for an unidentified specimen from Victoria all attributes were obtained by the author. It was found that older descriptions were usually imprecise and avoided definition of difficult systems such as nephridial and blood systems. More recent descriptions include a larger number of measured characteristics, and are based to some extent on an accepted descriptive format.

A list of attributes was drawn up for all plutelloid species described in three sets of literature:

(a) Australian material: Jamieson (1970, 1971a, 1972a, b, c and manuscripts), augmented where necessary and possible by Fletcher (1887, 1888, 1889), Spencer (1892, 1895, 1900), Jackson (1931), Sweet (1900) and the author's nephridial descriptions (Horan, 1971).

(b) American material: Macnab and McKey-Fender (1948, 1958, 1959 a, b), McKey-Fender (1957), and Gates (1941, 1962).

(c) Indian material: Gates (1945 a, b; 1961).

Thirty-seven morphological attributes, both external and internal, were selected as being cross-referrable in the Australian and American (Macnab and McKey-Fender) descriptions. As the Gates descriptions provided considerably less data, these were excluded from the study.

Forty-nine species for which sufficient codable information was available were chosen as O.T.U.'s (Operational Taxonomic Units). Table 1 gives the numbers used to identify O.T.U.'s, their original name, pre-revisional designation, and new grouping as given or proposed by Jamieson.

CODING OF ATTRIBUTES

The types of attributes described in the literature fell into three categories: two-state attributes, which could be simply coded in binary terms; metrical attributes (measurements, counts, and standardized measurements); and attributes with more than two possible states. The terminology of Lance and Williams (1967) was adopted, the three types being designated as qualitative, quantitative, and multistate respectively. A list of thirty-six of these attributes is given in Table 2. A thirty-seventh attribute, 'prostate morphology' was withheld tentatively, because of its previous emphasis as a 'key' character

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* Abbreviations used in Table 1.
    Pu: unrevised *Plutellus*; Wa: *Woodwardiella*; Pu (t): *Plutellus, toutellus* group; Pu (d): *Plutellus, davisi* group; Pu (A): *Plutellus, 'Argilophilus'* group.
    A: proposed reinstated *Argilophilus*; F: reinstated *Fletcherodrilus*; G(g): *Graliophilus, georgei* group; G(s): *Graliophilus, strelitzi* group; H: *Heteroporodrilus*; P: *Plutellus*, restricted; PP: affinities with *Plutellus*; S: *Simsia*; U: unrevised; W: *Woodwardiella*, restricted; <: junior synonym of.
    Names in quotation marks represent previously misidentified material.
† Now = *S. multituberculata* (Jamieson, 1972a).
‡ Subspecies of 10.

separating the genera *Plutellus* and *Woodwardiella*. It was planned to re-run using this character if it appeared that the study was prejudiced without it. Some of the multistate attributes used are non-exclusive (see Lance and Williams, 1967).

For the second task setal ratio attributes (quantitative attributes 1 to 4) were removed from consideration.

TABLE 2

ATTRIBUTES USED IN STUDY

QUALITATIVE

1.	Posterior setal arrangement	—	regular/irregular
2.	Shape of clitellum	—	annular/saddle-shaped
3.	Penial setae	—	presence/absence
4.	Position of last gizzard	—	segment V/segment VI
5.	Typhlosole	—	presence/absence
6.	Nephridial bladders	—	presence/absence
7.	Anterior tufted nephridia	—	presence/absence
8.	Testis sacs	—	presence/absence
9.	Arrangement of testes	—	metandric/holandric
10.	Supra-oesophageal vessel	—	single/double
11.	Position of last hearts	—	segment XII/segment XIII

QUANTITATIVE

1. Standardized setal ratio aa: circumference 100
2. Standardized setal ratio ab: circumference 100
3. Standardized setal ratio bc: circumference 100
4. Standardized setal ratio cd: circumference 100
5. Maximum number of segments occupied by clitellum
6. Number of segments containing spermathecal pores
7. Number of segments containing calciferous development
8. Number of latero-oesophageal hearts
9. Number of segments through which prostates extend
10. Ratio of spermathecal length: diverticulum length

MULTISTATE

1. Prostomial morphology—6 states:
   (i) prolobous   (iii) tanylobous   (v) epitanylobous
   (ii) epilobous   (iv) proepilobous
2. Body length—3 states:
   (i) small (less than 65 mm)   (ii) medium (65–200 mm)   (iii) large (more than 200 mm)
3. Position of first dorsal pore—3 states:
   (i) anterior pre-clitellar   (ii) immediate preclitellar to   (iii) immediate post-clitellar
       (3/4 to 7/8)   clitellar (9/10 to 14/15)   (18/19 to 20/21)
4. Nephropore arrangement—6 states:
   (i) single series 'C' lines   (iii) single series 'D' lines   (v) other alternation
   (ii) single series mid 'CD'   (iv) heteropore alternation   (vi) 'erratic' positioning
5. Clitellum position—4 states:
   (i) to segment XVIII   (iii) to segment XVI   (iv) to segment XIX
   (ii) to segment XVII
6. Female pore position—3 states:
   (i) anterior median to 'A'   (ii) anterior to 'A'   (iii) anterior lateral to 'A'

7. Male pore position—5 states:
    (i) on 'A'   (iii) on 'B'   (v) median to 'A'
    (ii) in 'AB'   (iv) lateral to 'B'

8. Spermathecal pore position—6 states:
    (i) median to 'A'   (iii) in 'AB'   (v) lateral to 'B'
    (ii) on 'A'   (iv) on 'B'   (vi) on 'C'

9. Morphology of calciferous glands—4 states:
    (i) no glandular development   (iii) extramural sessile glands (iv) extramural stalked glands
    (ii) some swelling and
         vascularization

10. Position of calciferous glands—6 states:
    (i) to segment XIII   (iii) to segment XV   (v) to segment XVII
    (ii) to segment XIV   (iv) to segment XVI   (vi) to segment XII

11. Origin of intestine—8 states:
    (i) segment XIV   (iv) segment XVII   (vii) segment XX
    (ii) segment XV   (v) segment XVIII   (viii) segment XXIV
    (iii) segment XVI   (vi) segment XIX

12. Position of nephridial tufts—6 states:
    (i) in segments II, III, IV   (iii) in segments V, VI, VII   (v) single pair in II
    (ii) in segments IV, V, VI   (iv) in segments V, VI   (vi) in segments II, III, IV, V

13. Position of seminal vesicles—7 states:
    (i) in segment XII   (iv) in segments X, XI   (vi) in segments IX, X, XI, XII
    (ii) in segments IX, X   (v) in segments XI, XII   (vii) in segments IX, XI, XII
    (iii) in segments IX, XII

14. Morphology of seminal vesicles—2 states:
    (i) racemose   (ii) tubular

15. Morphology of spermathecal diverticulum—6 states:
    (i) no diverticulum   (iii) 1 uniloculate diverticulum (v) 1 multiloculate diverticulum
    (ii) diverticulum intramural   (iv) 2 uniloculate diverticuli   (vi) 2 multi.oculate diverticuli

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PROGRAMMES

The programmes were chosen by Dr W. T. Williams, of C.S.I.R.O. Division of Tropical Pastures, Brisbane, from mixed data classificatory programmes designed by himself and Dr G. N. Lance, and available on the Control Data 3600 computer in Canberra. Two programmes were selected, and both were used for each task. These were the MULTBET programme, sorting by an information statistic strategy (Lance and Williams, 1967) and the MULTCLAS programme, as described by Lance and Williams (1967), but sorting by the increment in sum of squares strategy of Burr (1970). Both programmes employ agglomerative methods to supply a dendrogram; that is they create a hierarchical classification by a process of successive fusions of elements, based on some sort of difference measurement between the elements. In the information statistic strategy this difference is expressed as the information gain associated with the fusion; in the Burr strategy the elements are treated as points in a Euclidean space, and fusion occurs between pairs or clusters of elements whose combination provides the lowest increment in the sum of the squared Euclidean distances between the points and their centroid.

A second portrayal of the relationships obtained by the programme was given in each case by a basic ordination process, using the principal coordinates analysis of Gower (1966).

The print-out from each ordination consisted of coordinates 1 to 7. Of these, the first three coordinates were plotted.

Lance and Williams (1967) recommend the information statistic MULTBET strategy as the most suitable programme available at that time. The Burr strategy MULTCLAS programme has been developed since then, and compares favourably with the MULTBET (Williams, pers. com.). In the MULTBET programme, quantitative characters are treated as 'ordered' (i.e. ranked) multistates; in the Euclidean system, all characters are treated as metrical. The Burr strategy tends to be more accurate in its treatment of quantitative characters than does the information statistic strategy.

The MULTBET strategy has recently been found to show the phenomenon of 'group size dependence'—comparisons between groups are affected by a difference in size of the groups (Williams, Clifford and Lance, 1971). This effect increases with the square of the number of elements in a group, and thus will not be expected equally in all classifications obtained by this method. However, if a dendrogram contains groups of extremely unequal size at the same level, groupings at higher levels will be biased to some extent by group size dependence.

NUMBER AND NATURE OF ATTRIBUTES

The number of attributes used in tasks 1 and 2 (thirty-six) may appear small. Sims (1966, 1969) uses forty-three, Jamieson (1968) sixty-nine and Lee (1970) forty-six attributes. Two important differences between these and the present study stem from (a) the nature of the O.T.U.'s used, and (b) (in Jamieson's work) the nature of the coding.

> (a) O.T.U.'s: In Sims' (1966, 1969) paper, the O.T.U.'s are species, but the emphasis is not on their singularly 'species' nature; each species (in one case two species) is used to represent its higher taxon. Jamieson also uses species as O.T.U.'s, but as well as members of the group under investigation he uses as 'calibrators' species from other families. In both cases, gross differences can be expected in attributes which do not vary at lower taxonomic levels.
> Sims's work has been criticised by Lee on the grounds that the O.T.U.'s, though used as generic representatives, are actually no more than species, and thus the attributes used are predominately those of species. The suggestion is that a character-list from such an O.T.U. set would consist of finely differing species-characters, bolstered by grossly differing higher taxon-characters. Such a character-list could only be valid when large numbers of representative species were used for each genus chosen. This is the case in Lee's work, where 170 of the 178 New Zealand species of Megascolecids were used as O.T.U.'s.
>
> (b) Coding: As noted above, in Jamieson's analysis, some attributes which in the present paper are treated as a single multistate were broken into a number of two-state attributes.

The group chosen for study was homogeneous in regard to some attributes. It is considered that the attributes coded for the computations give a reasonable coverage of the varying morphological features, with some notable exceptions. In particular a larger number of blood system characteristics would have been preferred. The difficulties of cross

reference in character descriptions for the blood system can be attributed to the lack of a definitive work on this system, and also to the usually small series of specimens available for examination to revisers—the blood system is delicate and difficult to determine in preserved specimens.

RESULTS

PROGRAMME WITH ALL ATTRIBUTES

DENDROGRAMS: In the information statistic (Fig. 1), the first major groupings are of approximately equal status and size (except for one two-membered group). These can be summarized as follows:

(1) the unresolved Tasmanian *Plutellus tasmanianus*, the unresolved *P. tisdalli*, the two-membered *Plutellus* sens. strict., two *Heteroporodrilus*
(2) the remaining *Heteroporodrilus*
(3) all proposed reinstated *Argilophilus*
(4) seven *Simsia*, three *Graliophilus*, the unresolved *P. semicinctus*
(5) the remaining *Simsia* species
(6) reinstated *Fletcherodrilus*
(7) unresolved Victorian and Tasmanian *Plutellus*, one *Graliophilus*, the single included *Woodwardiella*

The next fusion combines each of the pairs 1-2, 4-5 and 6-7. The final fusion is between group 1-2 and the group formed of the remaining O.T.U.'s.

In the Euclidean dendrogram (Fig. 2) the first major groups vary more in size, but are approximately equal in status. These are as follows:

(1) reinstated *Fletcherodrilus*
(2) a single-membered group, the unresolved *P. tasmanianus*
(3) a group of unresolved *Plutellus*, constituting all except *P. macedonensis* of the unresolved *Plutellus* in group 7 of the information statistic programme
(4) *Plutellus* sens. strict., the unresolved *P. tisdalli*, *Paraplutellus insularis*—that is, part of group 1 in the information statistic strategy
(5) all *Heteroporodrilus*
(6) proposed reinstated *Argilophilus*
(7) five *Simsia* members
(8) *Graliophilus*, *strelitzi* group
(9) the remaining *Simsias*, two *Graliophilus* (*georgei* group)

In the succeeding fusions, groups 7-8-9, groups 4-5, and groups 1-2-3 become united, to form clusters close in constitution to clusters 4-5, 1-2, and 6-7 respectively in the information statistic dendrogram. Finally two large groups are formed, the one containing *Fletcherodrilus, Heteroporodrilus, Plutellus* sens. strict., *Paraplutellus*, and all unresolved *Plutellus* except *Plutellus macedonensis*, the other containing *Argilophilus, Simsia, Graliophilus, Woodwardiella molaeleonis*, and *P. macedonensis*.

ORDINATIONS: The GOWER ordinations, using the first three coordinates, for the information statistic programme are given in Fig. 3.

The strongest clustering occurs in the cases (a) entire proposed reinstated *Argilophilus* and (b) entire *Heteroporodrilus*, plus *Plutellus* sens. strict and *Paraplutellus insularis*. Within cluster (b) *Plutellus* and *Paraplutellus* become distinguished from the rest of the group in the third vector. O.T.U.'s 4 and 2 (*Fletcherodrilus fasciatus* and *Graliophilus candidus*) occur as separate entities. The remaining material forms one diffuse group in which, however, some unplaced *Plutellus*, O.T.U.'s 7, 9, 5, 21, 25, and 28 form a loose
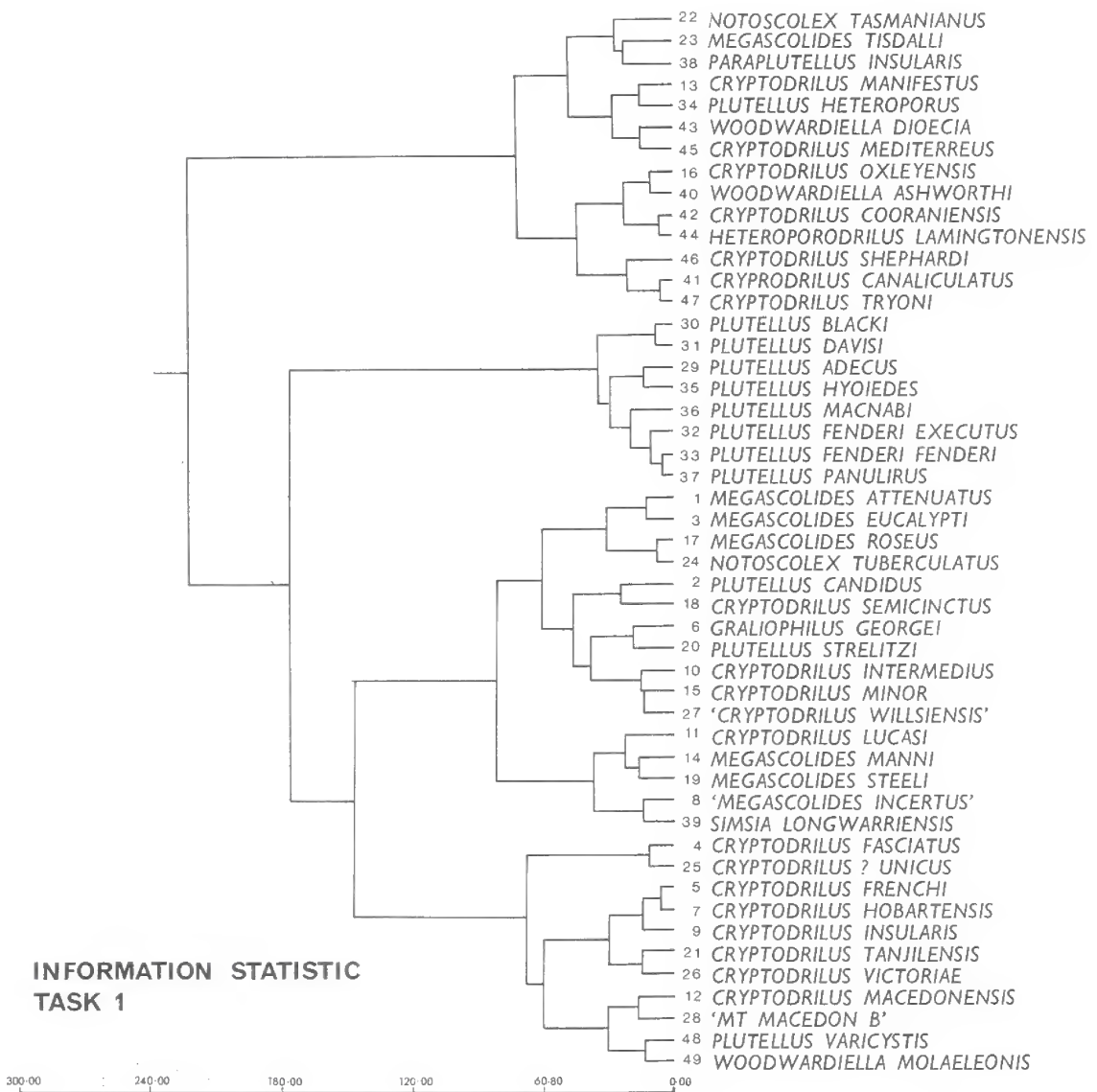
FIG. 1: Dendrogram of relationships among the 49 O.T.U.'s as determined by the information statistic strategy using 36 attributes.

'group' in that they do not mingle with the *Simsia* material: the remaining O.T.U.'s are scattered between these two loose groups.

The ordinations for the Euclidean programme are shown in Fig. 4. Here again distinct clusters are formed of the *Argilophilus* and *Heteroporodrilus-Plutellus* sens. strict.-*Paraplutellus* material. O.T.U.'s 2, 4 and 23 form a loose group in the principle coordinates ordination, with 2 (*Graliophilus candidus*) separating from the cluster on the third co-
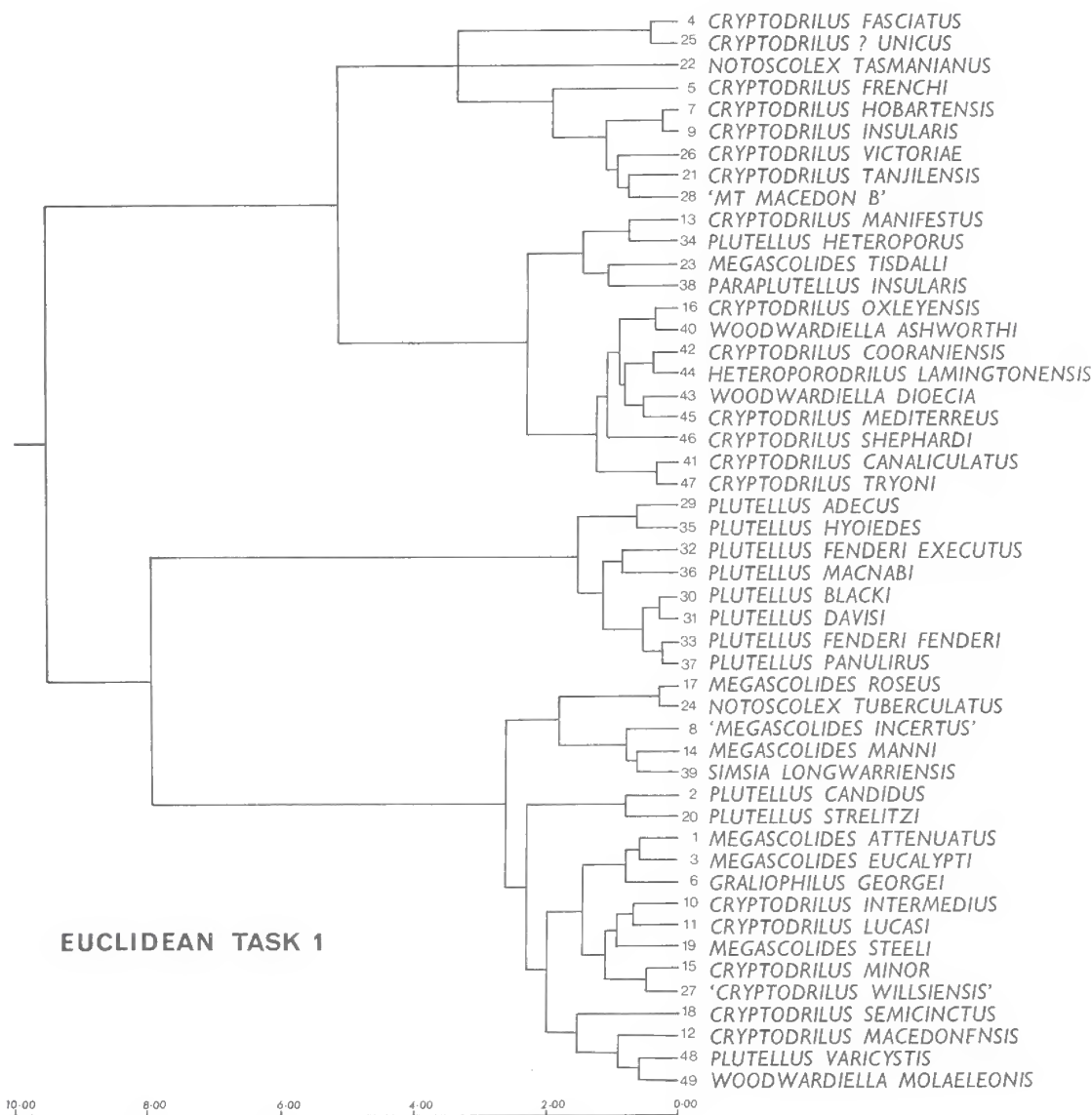
FIG. 2: Dendrogram of relationships among the 49 O.T.U.'s as determined by the Euclidean (increment in sum of squares) strategy, using 36 attributes.
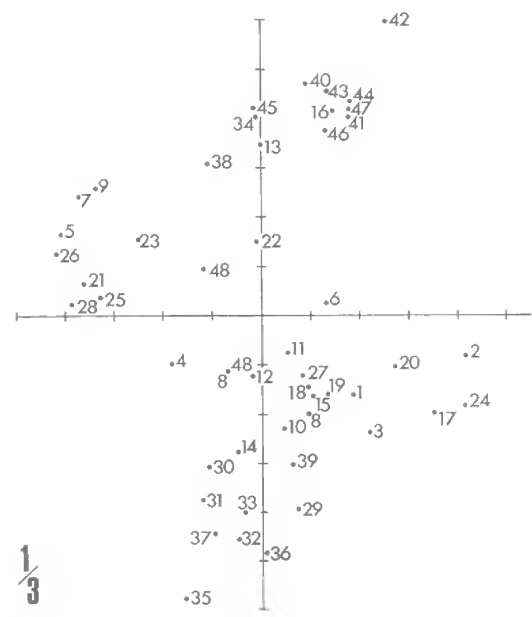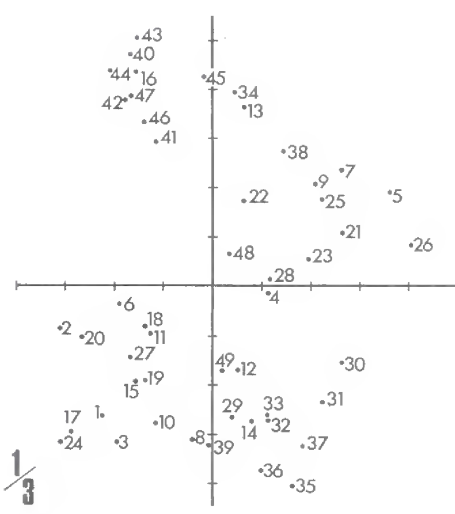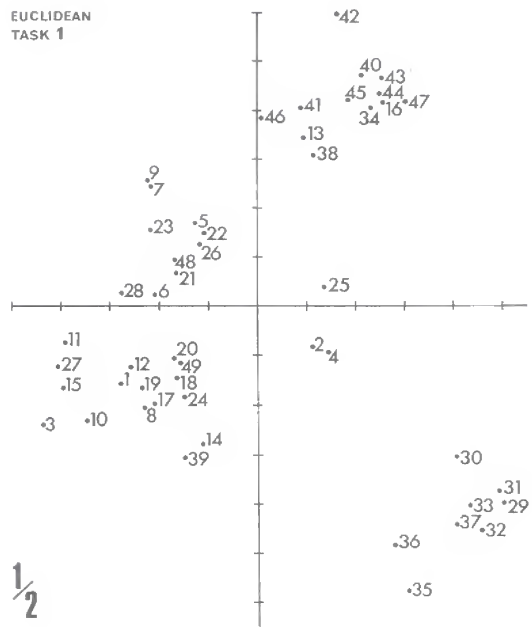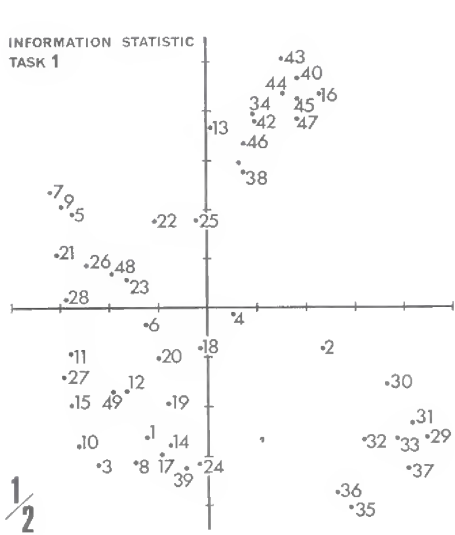
FIG. 3: GOWER ordination along three axes for the information statistic programme using 36 attributes. Numbers represent O.T.U.'s, as in text.

FIG. 4: GOWER ordination along three axes for the Euclidean (increment in sum of squares) programme using 36 attributes. Numbers represent O.T.U.'s, as in text.

ordinate. The *Simsia* material, plus O.T.U.'s 12, 18, 20, and 49 (*Plutellus macedonensis*, *P. semicinctus*, *Graliophilus strelitzi*, and *Woodwardiella molaeleonis*) form a loose cluster. The remaining material forms another loose cluster, close to this, with O.T.U.'s 7, 9, 5, 21 and 28 clustering on the third axis.

PROGRAMME OMITTING SETAL RATIOS

The dendrograms from the programmes which excluded setal ratio attributes are given in Fig. 5 (information statistic) and Fig. 6 (Euclidean).

At the numbered grouping levels, the structure of the Euclidean dendrogram remains almost unchanged. The single-membered group 2 of task 1 joins group 5, and some re-arrangements occur in groups 8 and 9. Membership of the two large groups is thus the same as in task 1, although the fusions forming the groups occur earlier in task 2 dendrograms.

In the information statistic, although the groupings at the numbered level remain little changed, the old group 6-7, minus O.T.U.'s 12, 48 and 49, is transferred from its combination with the *Simsia-Graliophilus-Argilophilus* group to join the *Heteroporodrilus-Plutellus* sens. strict.-*Paraplutellus* group. The dendrogram then agrees with the Euclidean dendrogram for both tasks. In the ordinations (Figs. 7, 8) no obvious alterations of the groupings in Figs. 3 and 4 are detectable.

DISCUSSION OF RESULTS

The strategies used provided some compact groupings essentially in harmony with groupings proposed by Jamieson. In interpreting dendrograms and also vector diagrams, consideration should be made of the following points: (a) visual analysis of graphic results can be biased to some extent by the size of the group; (b) small groups, in particular one-membered groups, will tend to be accommodated within adjacent groups, and thus lose identity; (c) because of the phenomenon of group-size dependence, particularly in the MULTBET programme (Williams, Clifford, and Lance, 1971) larger groups will tend to be better defined than smaller groups.

PROGRAMME WITH ALL ATTRIBUTES: The 'neatest' grouping is that of the North American O.T.U.'s. All American species included in the study are described by Macnab and McKey-Fender (between 1948 and 1959). Their work is thorough, usually based on large population samples and detailed examination of variation. In all sets of results for the present study, the North American species form a compact group, well separated from other groups, and with affinities within the group agreeing with those proposed by Macnab and McKey-Fender. Jamieson (1971c) suggests that reinstatement of Eisen's *Argilophilus* for these and other western North American *Plutellus* is justified. This move has not been proposed by Macnab and McKey-Fender, who do however regard this group as distinct from Perrier's *Plutellus*.

The results agree with the predicted affinities (Jamieson, 1971c, 1972a) of a *Plutellus* sens. strict.-*Paraplutellus-Heteroporodrilus* group, although some separation of *Plutellus* and *Paraplutellus* from *Heteroporodrilus* is visible, particularly in the ordinations. This separation would be enhanced by the inclusion of prostate morphology and a further

nephridial attribute in the attribute list. (In *Plutellus* sens. strict. and *Paraplutellus* alternation of nephropores between setal lines b and d commences on segment V or VI; in *Heteroporodrilus* this commences on segment X). Jamieson (pers. com.) suggests that separation of these O.T.U.'s into three genera is justified by the extra information so conveyed.

The members of Jamieson's newly-named genus *Simsia* (1972a, 1972b) do group together, but the grouping is not exclusive. This is mainly due to the enigmatic arrangement
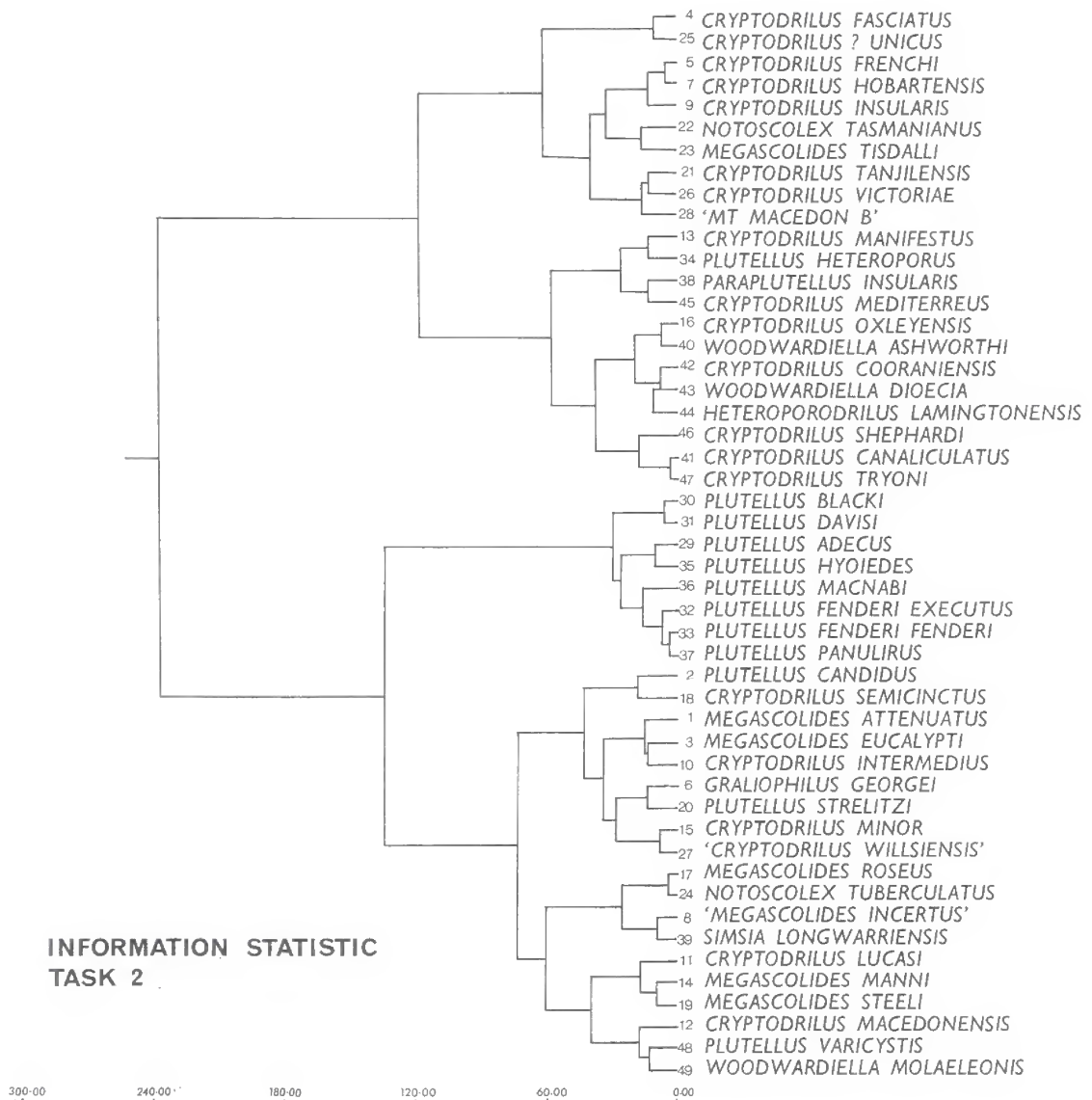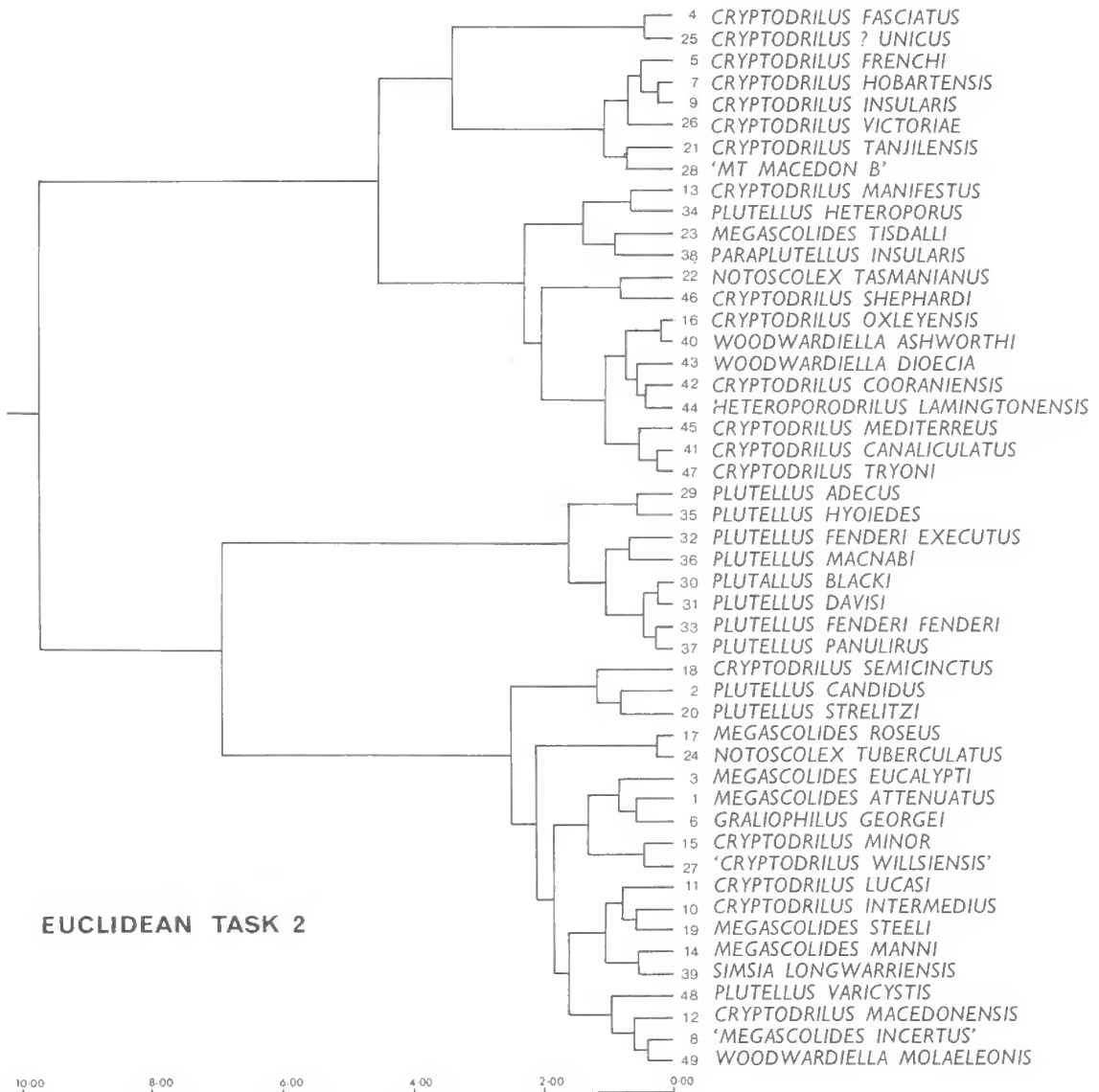

FIG. 5: Dendrogram of the relationships among the 49 O.T.U.'s as determined by the information statistic strategy, omitting the four setal ratio attributes.

of the Western Australian material, which is interspersed amongst the *Simsia* placings. As predicted by Jamieson (1970), *Woodwardiella molaeleonis* is well separated from the *Heteroporodrilus* group, formerly all included in *Woodwardiella*. *W. molaeleonis* pairs in both dendrograms with *Plutellus* (now *Graliophilus* Jamieson) *varicystis*. As only four members of the new genus *Graliophilus* were included in the study, their erratic placement could possibly be due to poor relationship with each other, and thus their inclusion in the group to which they are most similar (apparently the *Simsia* group). This could be tested

FIG. 6: Dendogram of the relationship among the 49 O.T.U.'s as determined by the Euclidean (increment in sum of squares) Strategy, omitting the four setal ratio attributes.
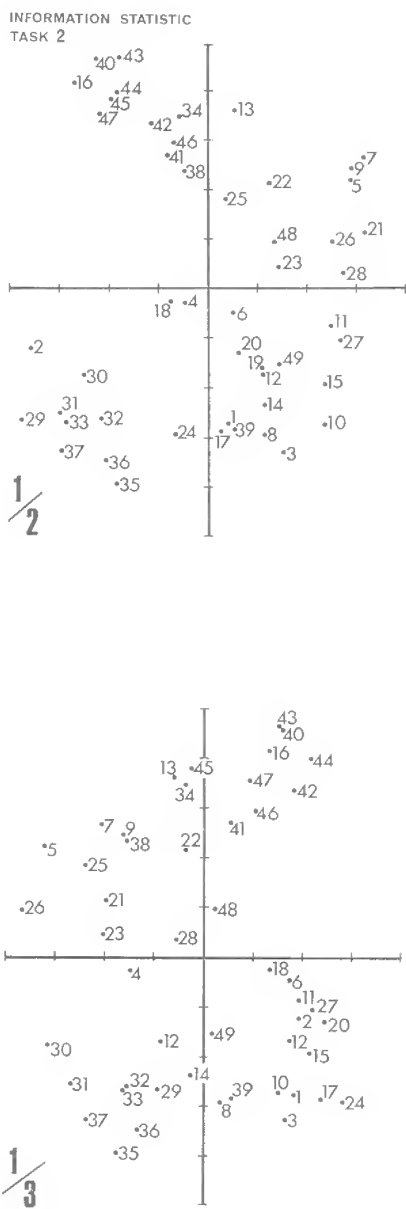
FIG. 7: GOWER ordination along three axes for the information statistic programme omitting the four setal ratio attributes. Numbers represent O.T.U.'s, as in text.
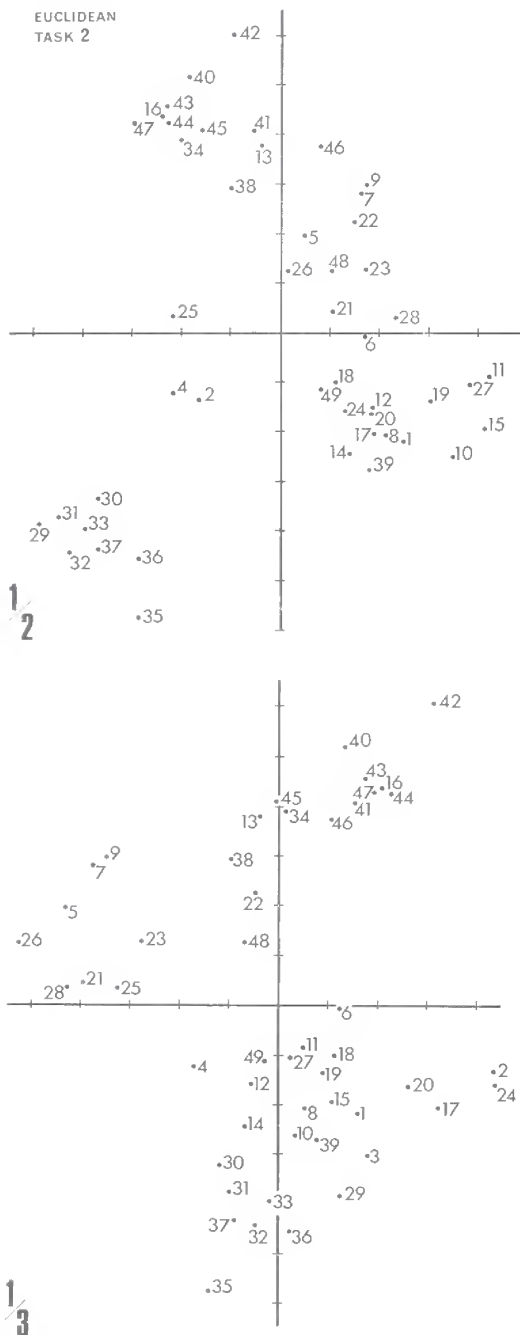
FIG. 8: GOWER ordination along three axes for the Euclidean (increment in sum of squares) programme omitting the four setal ratio attributes. Numbers represent O.T.U.'s, as in text.

by examination of a more exhaustive species list, which could exclude those O.T.U.'s with which *Graliophilus* and *Simsia* formed no fusions.

The two-membered reinstated *Fletcherodrilus* Michaelsen (Jamieson, 1970) remains as a reasonably well-isolated pair in both the dendrograms and the ordinations.

Placement of some of the unresolved *Plutellus* is erratic, but on the basis of the reasonable agreement obtained for most of the previously proposed groupings, it is suggested that a further group, comprising *Plutellus frenchi*, *Plutellus hobartensis*, *Plutellus insularis*, *Plutellus tanjilensis* and *Plutellus victoriae* (and the Mt Macedon specimen, which must be ignored until further specimens are found) could possibly be given status as a genus.

PROGRAMME OMITTING SETAL RATIOS: Removal of the four quantitative setal ratio attributes had very little effect on the groupings at the 'probably generic' level, and only a slight effect at the higher fusion levels. This tends to support the suggestion (Jamieson, 1972b, 1972d) that these attributes distinguish well between suprageneric groupings but less well between genera. As the intensity of clustering at the 'probably generic' level is little changed by their removal, it seems unlikely that in this case setal ratios are acting as a summary of overall phenetic similarity at this level; however, a separate programme, using setal ratios only, would be required to test this. It is possible that in this case they have a 'noise' function only.

DISCUSSION

With very few exceptions, species criteria in oligochaete descriptions are entirely morphological, and as is the case with many of the species of the plutelloid group, all that is known of a species is known from a few preserved specimens. Moss and Webster (1969, p. 423) point out that the same is true for the parasitic Nematoda:

> The biological species concept has, at present, little applicability to the field of parasitic nematology, an area in which species must be recognized almost entirely on the basis of anatomical evidence.

When this factor is coupled with the paucity of palaeontological evidence, it is clear that classifications will usually involve either interpretation of the evolutionary relevance of present structures, or consideration of similarities based on a range of characteristics.

The first approach was tried in the Oligochaeta, and the resulting classification perpetuated for fifty years before its highly unsatisfactory and artificial nature was challenged (see discussion in Lee, 1959, p. 31). Since Gates (1937), most oligochaete workers have favoured the second approach, sometimes referred to as 'intuitive'. It would seem obvious that computer methods provide the oligochaete taxonomist with more efficient, operationally definable means of carrying out the same task. The present work is considered to provide an example of this.

Coding difficulties experienced in the present work indicate that, if numerical techniques are to be used, descriptive formats will in future require standardization with this in mind. Ideally, before the phenetic approach is applied on a large scale to generic and super-generic levels in the Oligochaetes, it should be applied to questions of infraspecific variation and species limits.

ACKNOWLEDGEMENTS

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